

A new species of *Oeneis* from Alaska, United States, with notes on the *Oeneis chryxus* complex (Lepidoptera: Nymphalidae: Satyrinae)

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Abstract. *Oeneis tanana* A. Warren & Nakahara is described from the Tanana River Basin in southeastern Alaska, USA. This new taxon belongs to the *bore* group of *Oeneis* Hübner, [1819] and is apparently closest to *O. chryxus* (E. Doubleday, [1849]) by morphology, including its larger size and similarity of the female genitalia. In wing patterns and *COI* mitochondrial DNA barcode sequences, it is reminiscent of *O. bore* (Esper, 1789). A review of *O. chryxus* subspecies suggest that some may be better treated as species-level taxa. Evolutionary scenarios within the *chryxus* complex of taxa are discussed. While we hypothesize that *O. tanana* is best considered a species-level taxon, we have not identified any single character that unambiguously separates it from *O. chryxus*. Further study is needed to elucidate the species- or subspecies-level status of *O. tanana*, and to determine if it may have evolved through hybridization between *O. chryxus* and *O. bore*.

Key words: Beringia, butterflies, cryptic species, hybrid species, Nearctic, speciation, taxonomy, Yukon Territory.

INTRODUCTION

Butterflies of the genus *Oeneis* Hübner, [1819] are Holarctic in distribution, and occupy a wide range of habitat types, including montane and boreal forests, taiga, grasslands and steppe, alpine and arctic tundra, with several species occurring in sparsely vegetated, rocky terrain (*e.g.*, Ferris 1980; Troubridge et al.

1982). While the nomenclature of Nearctic members of *Oeneis* can be considered relatively stable (*e.g.*, dos Passos 1961, 1964; Miller & Brown 1981; Ferris 1989; Pelham 2008, 2015), new taxa continue to be described (Troubridge et al. 1982; Troubridge & Parshall 1988; Guppy & Shepard 2001; Scott 2006; Holland 2010), and some unresolved taxonomic issues remain (*e.g.*, Hassler & Feil 2002). However, a large number of unresolved taxonomic questions persist among the much richer fauna of Palaearctic *Oeneis*, where species-level boundaries in some groups remain poorly defined (*e.g.*, Murayama 1973; Lukhtanov 1983; Korshunov & Gorbunov 1995; Bogdanov et al. 1997; Gorbunov 2001; Korshunov 2002; Korshunov & Nikolaev 2003; Korb 2005; Chernov & Tatarinov 2006). Progress in improving our knowledge of relationships in *Oeneis* is nonetheless being made; a recent molecular study (Kleckova et al. 2015) has

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helped resolve many of the issues related to the composition of species groups in the genus, a process initiated over 120 years ago.

Elwes & Edwards (1893) were the first to investigate the morphology of the male genitalia of *Oeneis*. They noted that *O. chryxus* (E. Doubleday, [1849]), *O. alberta* Elwes, 1893, *O. bore* (Esper, 1789) and *O. taygete* Geyer, [1830] (now often considered conspecific with *O. bore*) all shared the presence of a similar “tooth” on the valvae, not found in other *Oeneis* species. Dos Passos (1949) referred to Nearctic taxa with this character as members of the “*taygete* group.” Based on this character, Gross (1970) united *O. bore*, *O. taygete*, *O. nevadensis* (C. Felder & R. Felder, 1867), *O. macounii* (W. H. Edwards, 1885), *O. chryxus*, *O. ivallda* (Mead, 1878), and *O. alberta* under “Gruppe C” in his review of the genus; this group of taxa was subsequently called the “*bore* group” by Lukhtanov (1984), Gorbunov (2001), Lukhtanov & Eitschberger (2001), Pelham (2008, 2015) and Kleckova et al. (2015). With the exception of various Palaearctic taxa associated with *O. bore*, *O. pansa* Cristoph, 1893 and *O. ammon* Elwes, 1899 (e.g., Korb 1998; Korshunov 2002; Korshunov & Nikolaev 2003; Tsvetkov 2006; Yakovlev 2011), the *bore* group is Nearctic in distribution.

The *Oeneis chryxus* complex currently includes nine taxa, which are usually considered to be subspecies of *O. chryxus* (e.g., Ferris 1989; Pelham 2008, 2015). These include *O. c. strigulosa* McDunnough, 1934 [Type Locality in Ontario], *O. c. calais* (Scudder, 1865) [Type Locality in Quebec], *O. c. caryi* Dyar, 1904 [Type Locality in NE Alberta], *O. c. chryxus* [Type Locality in W Alberta], *O. c. altacordillera* Scott, 2006 (Type Locality in Colorado), *O. c. socorro* R. Holland, 2010 [Type Locality in New Mexico], *O. c. valerata* Burdick, 1958 [Type Locality in the Olympic Peninsula, Washington], *O. c. ivallda* [Type Locality in Placer County, California] and *O. c. stanislaus* Hovanitz, 1937 [Type Locality in Alpine County, California]. Since 2006, however, some authors have recognized more than one species-level taxon in the *chryxus* complex, as detailed below (see Discussion).

While curating the genus *Oeneis* in 2010 at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, ADW encountered a series of distinctive Alaskan specimens, collected near the town of Tok in the southeastern part of the state, which had previously been determined as *O. chryxus*. The large size and overall dark aspect of these specimens contrasted sharply with other populations of *O. chryxus*. A brief review of the male genitalia by JPP and ADW in 2011 confirmed the placement of these *Oeneis* in the *bore* group. A subsequent search of the Kenelm Philip collection

(currently housed at the University of Alaska Museum, Fairbanks) by ADW and KMD in 2015 revealed a large number of additional specimens from multiple localities bordering the Tanana River in southeastern Alaska. Further searches revealed many additional specimens in private collections, especially those of CDF and Jack Harry, the latter recently donated to the McGuire Center.

In an effort to determine the taxonomic status of these Alaskan specimens, genitalia of males and females were compared to those of *O. chryxus* from Yukon Territory and *O. bore* from Alaska. In addition, legs were sampled from all North American taxa in the *bore* group (except *O. c. socorro*) by VL in 2011 and NVG in 2015, from which sequence data from the “barcode” region of *COI* were obtained. Herein we present the results of these studies, and describe the distinctive Alaskan *Oeneis* as a new species, yet note that further elucidation of its taxonomic status is needed (see Discussion).

MATERIALS AND METHODS

Specimens examined are deposited in the following collections: private collection of Clifford D. Ferris, Laramie, Wyoming, USA (CDF); Private collection of Jim P. Brock, Tucson, Arizona, USA (JPB); Kenelm W. Philip collection, currently housed at the University of Alaska Museum, Fairbanks, Alaska, USA (as of January, 2016) (KWP); private collection of Martin Cesanek, Bratislava, Slovakia (MC); McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (MGCL); Triplehorn Insect Collection, Ohio State University, Columbus, Ohio, USA; material recently acquired from David Parshall, photos examined (OSUC).

Full data are provided for all specimens examined of the new species (see Types section, below), as well as for all specimens of *O. chryxus* from Alaska (6), British Columbia (103), and Yukon Territory (466), more-or-less as presented on specimen labels (see Additional Material Examined). Information between brackets “[]” in the listing of specimen data represents additional or corrected information. We also examined 3,670 additional specimens of the *O. chryxus* complex (as defined above) in the MGCL, as follows: Michigan (215), Wisconsin (24), Quebec (7), Ontario (391), Manitoba (177), Saskatchewan (2), Northwest Territories (5), Alberta (183), Montana (111), Wyoming (461), Colorado (862 *chryxus* + *altacordillera*), New Mexico (44), Utah (159), Nevada (65 *chryxus*, 93 *ivallda*), Idaho (119), Washington (142 *valerata*, 48 *chryxus*), California (562).

The distribution map (Fig. 7) was generated using SimpleMappr (<<http://www.simplemappr.net>>) based on existing locality information and additional data. When not provided on specimen labels, coordinates were estimated using Google Earth, often in combination with details provided in The Milepost (Morris 2015). All known localities from Alaska are included on the map, as are most localities in Yukon Territory, although a few localities from Yukon Territory that we have thus far been unable to pinpoint have not been mapped.

Wing lengths were measured with a digital Vernier caliper, from base to greatest length at the apex of the right forewing. Adult abdomens, legs, and palpi were soaked in hot KOH for 3-10 min prior to dissection, dissected, and subsequently stored in glycerine. Chlorazol black was used to stain female genitalia. Dissected specimens are indicated by "SN" numbers in the list of specimen data. External and genitalic morphology was studied using a Leica MZ 16 stereomicroscope and drawings were produced with a camera lucida attached to the Leica MZ 16 stereomicroscope. The terminology for wing venation follows the Comstock-Needham system described in Miller (1970), and the terminology for wing pattern elements follows Peña & Lamas (2005). Nomenclature of the genitalia mostly follows Klots (1956), but we follow Peña & Lamas (2005) in using the term aedeagus, and Muschamp (1915) in using the term 'brachia' for structures often called the 'gnathos'. Finally, we follow Austin & Mielke (2008) in referring to the part of the genitalia typically termed the 'vinculum' as 'combined ventral arms of tegumen and dorsal arms of saccus'.

Standard *COI* barcodes (658-bp 5' segment of mitochondrial *cytochrome oxidase subunit I*) were studied. *COI* sequences were obtained from 53 specimens representing the following species: *O. bore*, *O. chryxus*, *O. macounii*, *O. nevadensis*, *O. ammon* and the new species described below. We did not include *O. alberta* in the final *COI* analysis as this species is very distinct from both *O. bore* and the *O. chryxus* complex with respect to morphology and ecology, though it shares its barcodes with other members of the *O. bore* group (most likely due to a mitochondrial introgression). Legs from the samples labeled by letters BPAL and CCDB (43 specimens) were processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) using the standard high-throughput protocol described in deWaard et al. (2008). DNA was extracted from a single leg

removed from each voucher specimen employing a standard DNA barcode glass fiber protocol (Ivanova et al. 2006). All polymerase chain reactions (PCR) and DNA sequencing were carried out following standard DNA barcoding procedures for Lepidoptera as described by Hajibabaei et al. (2005). This set of voucher specimens is housed at MGCL, and can be identified by the corresponding unique BOLD Process IDs that were automatically generated by BOLD (Barcode of Life Data System). Photographs of these specimens are available in BOLD at <<http://www.barcodinglife.org/>>. Legs from the samples labeled with the letters NVG and OSUC were processed in the Grishin lab using Macherey-Nagel (MN) NucleoSpin® tissue kit according to the protocol described in Cong & Grishin (2014). The following pairs of primers were used to amplify the barcode in two overlapping segments: sCOIF (forward, 5'-ATTCAACCAATCATAAAGATAT-TGG-3') -Ven-m2COIR (reverse, 5'-GGTAAACTGT-TCATCCTGTTC3'), and Meg-mCOIF2 (forward, 5'-CCTCGWATAAATAAYATAAGATTTTG-3') -sCOIR (reverse, 5'-TAAACTTCTGGATGTCCAAAAAAT-CA-3'). NVG voucher specimens are housed at MGCL, except OSUC vouchers are at OSUC. Newly generated sequences and accompanying data were submitted to GenBank and received accession numbers KU552034-KU552042 and KU570409-KU570424.

The barcode analysis involved 74 *COI* sequences (including eight *O. norna* samples that were selected as an outgroup). Among them there were 21 published sequences (Lukhtanov et al. 2009; Pohl et al. 2009; Dewaard et al. 2014a,b; Kleckova et al. 2015) downloaded from GenBank. Sequences were aligned using BioEdit software (Hall 1999) and edited manually. Phylogenetic hypotheses were inferred using Bayesian methods as described previously (Vershina & Lukhtanov 2010; Talavera et al. 2013). Briefly, Bayesian analyses were performed using the program MrBayes 3.2 (Ronquist et al. 2012) with default settings as suggested by Mesquite (Maddison & Maddison 2015): burn-in=0.25, nst=6 (GTR + I + G). Two runs of 10,000,000 generations with four chains (one cold and three heated) were performed. Chains were sampled every 10,000 generations. The average value of the Potential Scale Reduction Factor (PSRF) was 1.000 and the average standard deviation of split frequencies was 0.009516 to the end of the analysis, indicating that convergence was achieved, and a good sample from the posterior probability distribution was obtained. The consensus of the obtained trees was visualized using software FigTree v 1.3.1 (Rambaut 2009).

RESULTS

Oeneis tanana A. Warren & Nakahara, sp. nov.

(Figs. 1, 3-4, 6a-c)

Zoobank LSID: urn:lsid:zoobank.org:act:AC40896F-1D0B-4090-A52F-94EBD739D62F

MALE. Head: Eyes brownish, naked; labial palpi (Figs. 3d,e) first segment short, covered with long dark-brown hair-like modified scales ventrally, 3-4 times as long as segment width, white scales laterally, longer white hair-like scales dorsally; second segment similar to first in scale orientation, about three times longer than first segment; third segment similar to first and second segments in scale orientation, shorter than first segment in male, same length in female; antennae approximately two-fifths length of forewing costa, 40 segments ($n=1$), pedicel about half as long as scape, with distal 15-16 segments comprising club. **Thorax:** Dorsally black, covered with golden hair-like modified scales; ventrally black, golden hair-like modified scales sparse. **Legs** (Figs. 3b,c): Foreleg tarsus slightly longer than tibia, femur slightly shorter than tibia; midleg and hindleg similar in length; femur black, adorned with long dark-brown hair-like modified scales ventrally, greyish scales scattered dorsally; tarsus and tibia of midleg and hindleg covered with greyish scales, dark brown hair-like modified scales present on distal half of tibia, tibia and tarsus adorned with spines, pair of relatively short tibial spurs located at ventral side of distal end of tibia. **Abdomen:** Eighth tergite elongated, approximately 1.5 times longer than seventh tergite, dorsal surface apparently weakly sclerotized; eighth sternite small, approximately two-thirds length of seventh sternite, apparently uniformly sclerotized.

Genitalia (Figs. 4a-e): Tegumen shaped somewhat like a 'megaphone' in lateral view, dorsal margin of tegumen slightly concave; uncus tapered towards end, slightly curved in lateral view, curved posterior end of uncus rounded in lateral view, slightly longer than dorsal margin of tegumen in lateral view, dorsally setoseous; brachia almost parallel to uncus in dorsal view, apex slightly hooked, roughly half length of uncus; ventral arms of tegumen partially fused to anterior margin of tegumen, thus form of anterior edge of tegumen somewhat like a plate in dorsal or posterior view; appendix angularis present; saccus relatively short, similar in length to brachia, dorsal arms of saccus combined with ventral arms of tegumen; juxta present; valva with scattered setae, positioned at approximately 30° angle to horizontal, distal half of valva roughly trapezoidal in lateral view with angular apex, 'tooth' present at middle section of dorsal margin of valva in lateral view, middle section of ventral margin of valva convex in lateral view, basal one third of dorsal margin concave; aedeagus similar in length to tegumen plus uncus, almost straight in lateral view, adorned with a variable number of short spines, open anterodorsally.

Wing venation and shape (Fig. 3a): Mean forewing length = 26.7 mm ($n=20$). Forewing recurrent vein absent; basal swelling of forewing cubital vein absent; hindwing humeral vein developed; shape typical of other members of the *O. chryxus* complex. **Wing pattern** (Figs. 1a-l): **Dorsal forewing** ground color dark brown; androconial dark scales approximately 1mm in width, present at distal end of discal cell along cubital vein, base of cells M_3 , Cu_1 and Cu_2 ; color and density of androconial scales highly variable; black submarginal ocellus in cell M_1 often with indistinct creamy pupil in center; submarginal ocelli variably present in cells M_3 , Cu_1 , with or without pale pupils; submarginal and margin of forewing variably overscaled with reddish or pale ochre, sparse or absent over and adjacent to wing veins, creating a series of irregularly-shaped patches separated by dark wing veins; fringe scales white and greyish. **Dorsal hindwing** ground colour same as forewing, with variable intensity of reddish or pale ochre overscaling; black ocellus in cell Cu_1 variable in development, from bold to absent, often with indistinct creamy pupil in center; fringe scales white and

greyish. **Ventral forewing** ground colour greyish-ochre; costal region (area basal to subcostal vein) mosaic of black and white, extending to apex, then along margin to cell R_5 , and variably to cells M_2 or M_3 ; numerous dark brown fragmented markings in discal cell, dark brown streak along M_2 - M_3 ; dark brown undulating band extending from costa, distal to discal cell, fading distally in cell M_2 , curved inwards below M_3 and extending to cell Cu_2 ; black ocellus in cell M_1 generally with creamy pupil in center; ocelli in cells M_3 and Cu_1 variably present, smallest in M_3 , with or without pale pupil; outer margin of forewing darker; fringe as described for upperside. **Ventral hindwing** ground colour indiscernible; wing veins highlighted with a variable amount of whitish scaling; costal region (area above subcostal vein) mosaic of black and white, extending along length of costa; pattern elements as follows, from base to distal margin: basal area mosaic of dark brown irregular markings with dark ochre background, followed by a whitish area with sparse dark brown irregular markings; dark brown sinuate band extending from costa to outer margin, approximately 1mm in width, roughly traversing in an outward direction until cubital vein, then roughly inward below cubital vein; area distal to this band mosaic of dark brown irregular fragmented markings with dark ochre and/or greyish white ground colour; second dark brown sinuate band extending from costa to outer margin, similar in width to previous band, roughly traversing in outward direction until origin of M_3 , then roughly inward below this point; area distal to this band broadly white, wider than previous band; area distal to this (submargin and margin) mosaic of dark brown irregular fragmented markings with dark ochre and/or greyish ground color, darkest along margin; trace of pale submarginal ocelli variably present in cells R_5 , M_1 , M_2 and M_3 , black ocellus in cell Cu_1 variably present, often with creamy pupil in center; fringe as described above.

FEMALE. Similar to male, except as follows: foretarsus not segmented although adorned with spines; mean forewing length = 26.9 mm ($n=10$); wing shape rounder and broader, lacking forewing androconia and surrounding darkened area. **Genitalia** (Figs. 4f-h): Lamella antevaginalis well developed, vertical projection under ostium bursae present and sclerotized, anterior portion of lamella antevaginalis forming a plate below this vertical projection; weakly sclerotised ventral region present in seventh and eighth intersegmental membrane, apparently fused with anterior portion of lamella antevaginalis; most of ductus bursae sclerotised; ductus seminalis located at base (posterior end) of corpus bursae; corpus bursae roughly oval, extending to third abdominal segment; two brown signa located at ventral side of corpus bursae, signa prominent and parallel to each other, spines of signa developed.

COI 'Barcode' sequence: vouchers CCDB-05786 D08, KWP:Ento:29760, NVG-5202, NVG-5203, 658 base pairs:

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AACTTTATATTTTATTTTAGGAATTTGAGCAG
GTATAGTAGGAACATCTCTTAGTCTTATTATTC
GAACAGAATTAGGTAACCCAGGATCTTTAATTG
GAAATGACCAAATTTATAACTATTGTTACAGCT
CATGCTTTTATTATAATTTTTTTTATAGTTATAC
CAATTATAATTGGGGGATTTGGAAATTGACTAAT
TCCTCTAATACTTGGAGCCCCTGATATAGCCTTC
CCCGAATAATAATAATAAGATTTTGACTTTTAC
CCCTTCTTTGATACTTTTAAATTTCAAGCAATAT
TGTTGAAAATGGAGTAGGAACAGGATGAACAATT
TACCCCTCTCTCATCTAATATTGCCATAGAG
GATCTTCTGTTGATTTAGCAATTTTTTCTTTA
CATTTAGCTGGAATTTCTTCTATTTTAGGAGCT
ATTAATTTTATTACAACAATTTAATATACGAAT
TAATAATATAACTTATGATCAAATACCTTTATTT
GTTTGAGCTGTAGGAATTACAGCTTTATTATT
ATTACTCTCTTCTCTGATTAGCTGGGGCAAT
CACTATACTTCTTACAGATCGAAATTTAAATACT
TCATTTTTTGATCCAGCAGGAGGGGGAGACCCT
ATTTTATATCAACATTTATTT

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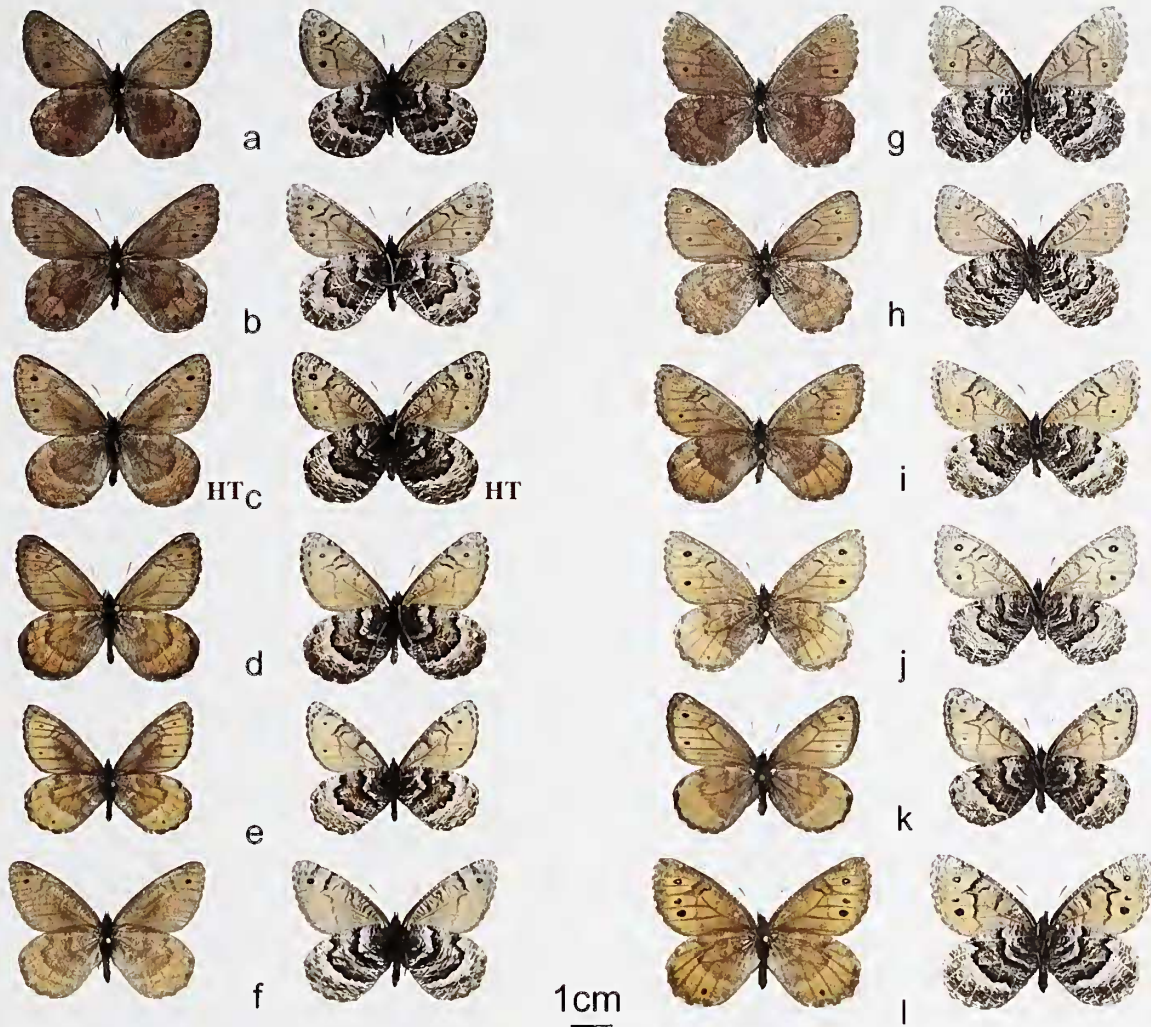


Figure 1. Males (a-f) and females (g-l) of *Oeneis tanana* from the type locality, 5 mi. S of Tok, Alaska, showing individual variation observed in the population. Each specimen is figured in dorsal (left) and ventral (right) views. HT = holotype. Specimens collected by M. Douglas (a-e, g-k, 17-18 June 1999) and J. Harry (f, 10 June 1999; l, 17 June 1999), in MGCL.

Types. Holotype male (Fig. 1c) with the following labels: white, printed: AK: TANANA VALLEY / 5 MI. S. OF TOK, TOK / CUT-OFF AT BUTCH / KUTH RD. V1-17-18-99 / LEG. M.G. Douglas /; white printed: J. D. Turner ex / Malcolm Douglas / colln. / MGCL Accession # 2009-26 /; red, printed: HOLOTYPE / *Oeneis tanana* / A. Warren & Nakahara /. The holotype is deposited in the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida (MGCL). Paratypes (326♂, 79♀) from: USA: ALASKA: Alaska Hwy., mi. 1270, 2000', 11-VI-1999, J. L. Harry (9♂, 1♀ MGCL); Alaska Hwy. (Hwy. 2), mi. 1289.55, 63°13.9'N 142°17.9'W, 1800', 15-VI-1997, C. D. Ferris (13♂, 1♀ CDF); Alaska Hwy., mi. 1289.55, Midway Lake, gravel flats on hillside above road, 15-VI-1997, K. W. Philip (7♂, 2♀ KWP; UAM100190535-UAM100190543); Alaska Hwy., mi. 1316, 20-VI-1995, J. & F. Preston (1♂ MGCL); Alaska Hwy. (Hwy. 2), mi. 1354.2, 1800', 63°35'N 143°55'W, 15-VI-1995, C. D. Ferris (2♀ CDF); Alaska Hwy., mi. 1371, 28-VI-1970 (1♀ MGCL); Alaska Hwy. (Hwy. 2), mi. 1410, 1250', 61°56.7'N 145°23.7'W, 15-VI-1995, C. D. Ferris (1♂,

1♀ CDF); Alaska Hwy., mi. 1410, Spruce Road, powerline cut in taiga, grass and flowers, 1240', 17-VI-1997, K. W. Philip (2♂ KWP; UAM100060877, UAM100060878); Alaska Hwy., mi. 1410, 12 mi. SE Delta Jct., 1200', 15-VI-2001, J. L. Harry (1♀ MGCL); Anderson, 1 mi. E, 500', 4-VI-1999, J. L. Harry (1♂, MGCL); Hwy. 1, 5 mi. S Tok, 1700', 10-VI-1999, J. L. Harry (18♂, 2♀ MGCL); 12-VI-1999, J. L. Harry (21♂ MGCL); 13-VI-1999, J. L. Harry (13♂ MGCL); 17-VI-1999, J. L. Harry (26♂, 6♀ MGCL); 18-VI-1999, J. L. Harry (1♂, 1♀ MGCL); Hwy. 1, 5 mi. S of Tok, 1700', 63°16'N 143°02'W, 13-VI-1995, C. D. Ferris (2♂, 1♀ MGCL SN-15-145-♂, SN-15-155-♂, SN-15-149-♀); 14-VI-1995, C. D. Ferris (8♂ MGCL; incl. SN-15-147, SN-15-154, SN-15-156, SN-15-157); 14-15-VI-1995, C. D. Ferris (46♂, 17♀ CDF); 6-VII-1995 C. D. Ferris (1♀ MGCL, SN-15-151); Hwy. 1, 5.0 ± 0.5 mi. S of Tok, [1700'], 63°16.04'N 143°01.9'W, 5-VI-1997, C. D. Ferris (1♂, 1♀ CDF); 14-VI-1997, C. D. Ferris (52♂, 21♀ CDF); 1-VII-1997, C. D. Ferris (3♂, 4♀ CDF); Nenana, 400' [351'], 4-VI-1999, J. L. Harry (6♂ MGCL); 6-VI-1999, J. L. Harry (1♂ MGCL); Northway Airport, 1700', 11-VI-1999, J. L. Harry (1♂ MGCL);

Northway Airport, 7 mi. off Alaska Hwy., flower-filled lawns and fields, 1700', 15-VI-1997, K. W. Philip (1♀ KWP UAM100190552); Old Alaska Hwy., 3 mi. NE Tok, 1600', 12-VI-1999, J. L. Harry (2♂ MGCL); Richardson Hwy., mi. 229 [vic. Black Rapids], [2083'], 26-VI-1971, C. D. Ferris (1♀ CDF); Tanana River, 21 mi. SW Fairbanks, 400' [Bonanza Creek Experimental Forest], 18-V-1997, J. L. Harry (1♀ MGCL); Tanana Valley, 5 mi. S of Tok, Tok Cutoff at Butch Kuth Rd., 17-18-VI-1999, M. Douglas (53♂, 7♀ MGCL); Tok, 17-VI-1971, L. Jennings (1♂ KWP; UAM100379347); 9-VI-2005, Szymczyk (1♂ JPB); Tok Cutoff, 5 mi. S of Tok, Butch Kuth Ave., roadside flowers in open aspen/spruce forest, 13-VI-1995, K. W. Philip (11♂, 3♀ KWP; UAM100379326-UAM100379329, UAM100379344-UAM100379346, UAM100379367-UAM100379369, UAM100379384-UAM100379387); 14-VI-1995, K. W. Philip (25♂, 3♀ KWP; UAM100379330-UAM100379343, UAM100379370-UAM100379383).

Additional material examined

Oeneis tanana: "nr. Nome, Alaska", no date, no collector indicated (1♀ MGCL). This specimen was not included in the type series, since it is the only known specimen of *O. tanana* labeled from outside the Tanana River drainage, and it lacks the collection date and name of the collector; we suspect it is mislabeled. Considerable collecting efforts have been made in the Nome area, yet no material of *O. tanana* has been reported.

Oeneis chryxus: CANADA: BRITISH COLUMBIA (74♂, 29♀): Alaska Hwy. km. 600, 11-VII-1984, J. & F. Preston (1♂ MGCL); Alaska Hwy., mi. 392, mountain S of Summit Pass, 4000-7000', 22-VII-1948, W. Hovanitz (1♀ MGCL); Alaska Hwy., mi. 400, Summit Lake, 4200-5000', W. Hovanitz (2♂, 2♀ MGCL); Alaska Hwy., mi. 409, McDonald Ck., 6-VII-1948, W. Hovanitz (2♂ MGCL); Alaska Hwy. mi. 415, Racing R., 6-VII-1948, W. Hovanitz (4♀ MGCL); Alaska Hwy., MP 417, 18-VI-1970, A. O. Detmar (1♂ MGCL); Atlin, 600-900m, 22-VI-1991, J. Reichel (1♂, 1♀ MGCL); Atlin, 800m, 26-VI-1991 (1♂ MGCL); 23-VI-1991 (1♀ MGCL); Atlin Rd., 3 mi. N of Atlin, 2300', 30-VI-1985, C. D. Ferris (4♂, CDF); Atlin Rd., 3 mi. N of Atlin to Snafu Creek, 30-VI-1985, C. D. Ferris (1♂ CDF); Coalmount, 5-VII-1968, S. Shigematsu (4♂ MGCL); Crater Mtn., W of Keremos, 1-VII-1981, C. D. Ferris (2♂ CDF); Creston, Thompson Pk., 15-VII-1976 (3♂ MGCL); Gibson Pass, Manning Park, 5000', 16-VII-1979, C. Guppy (2♂ MGCL); 23-VII-1983 (1♂ MGCL); Haines Hwy., mi. 78, 4-VII-1971, C. D. Ferris (7♂, 1♀ CDF); Jct. of Cassiar Hwy. & Boya Lake Rd., 2200', 10-VI-1986, C. D. Ferris (12♂, 4♀ CDF); Kelly Lake - Canoe Creek Rd., nr. Jesmond, 3100-4400', 23-VII-1984, J. & F. Preston (2♀ MGCL); 24-VIII-1984, J. & F. Preston (1♂, 1♀ MGCL); [Manning] Park, 5000', Valley View, 7-VII-1961, H. Kimmich (1♀ MGCL); Mt. Princeton, 29-30-V-1964, H. Kimmich (1♂ MGCL); Otter Lake C.G., nr. Princeton, 9-VII-1976 (2♂, 1♀ MGCL); Pavilion - Kelly Lake Rd. at Diamond S Ranch, N of Lillooet, 3900', 24-VII-1984, J. & F. Preston (1♂ MGCL); Pavilion - Kelly Lake Rd., 8.5 mi. N Pavilion, 4300', 24-VII-1984, J. & F. Preston (2♂, 3♀ MGCL); Pink Mtn., halfway up, on road to lookout, 4-VII-1985, C. D. Ferris (2♂ CDF); Pink Mtn., mi. 147, Alcan Hwy., 9-VII-1978 (2♂ MGCL); Pink Mtn., mi. 147, Hwy. 97, 5000', VI-VII-1980, N. Tremblay (1♀ MGCL); Princeton, 27-VI-1966 (1♂ MGCL); Princeton, Cardinal Ranch, 27-VI-1966, B. Weber (1♀ MGCL); Stag Leap Cyn., Kootenay Dist., 27-VII-1987, D. L. Bauer (1♂ MGCL); Summerland area, Okanagan Valley, 25-VI-1983, J. Reichel (1♂ MGCL); Tompson Mt., Kootenay Dist., 25-VII-1981, D. L. Bauer (2♂ MGCL); 5 mi. S Clinton, 26-VI-1964 (14♂, 5♀ MGCL).

YUKON TERRITORY (317♂, 149♀): Alaska Hwy., bog nr. Johnson's Crossing, 22-VI-1948 (1♂, 1♀ MGCL); Alaska Hwy., mi. 825, 15-VI-1957, J. & F. Preston (1♂ MGCL); Alaska Hwy., mi. 895-900, nr. Whitehorse, 22-VI-1948 (1♀ MGCL; SN-15-152);

Alaska Hwy., mi. 976, nr. Mendenhall, 23-VI-1948 (2♂ MGCL); Campbell Hwy., km. 521, 1800', 12-VI-1979, J. & F. Preston (1♂ MGCL); Campbell Hwy., km. 533, 1700', 12-VI-1979, J. & F. Preston (13♂, 10♀ MGCL); Campbell Hwy., km. 563, 1400', 12-VI-1979, J. & F. Preston (1♂ MGCL); Campbell Hwy., km. 564-568, nr. Carmacks, 62°03'54.24"N 135°57'00.94"W, 560-650m, 11-VI-2008, M. Cesanek (15♂, 5♀ MC); Carcross Desert area, Hwy. 2 (Klondike Hwy.), in open woods at desert edge, 2170', 60°14'14"N 134°41'41"W, 29-VI-1985, C. D. Ferris (10♂, 2♀ CDF); Dawson, 13-VI-1911, ex Barnes coll., "holotype" of "yukonensis" (1♂ MGCL); 14-VI-1911, ex Barnes coll., "allotype" of "yukonensis" (1♀ MGCL); 10-VI-1981, N. Tremblay (30♂, 8♀ MGCL); Dawson Hwy., mi. 12.6, 16-VI-1962, J. Legge (1♂ MGCL); Dawson-Mayo Loop, mi. 69, W of Whitehorse, 21-VI-1970, D. Eff (2♂ MGCL); Dempster Hwy., mi. 10, 10-VI-1981, J. Johnstone (1♂ MGCL; 1♂ OSUC 618404); 10-VI-1981, N. Tremblay (22♂, 4♀ MGCL; 3♂, 9♀ OSUC 618391-618399, 618401-618403); 10-11-VI-1981, N. Tremblay (2♂ MGCL); 11-VI-1981, N. Tremblay (4♂, 2♀ MGCL; 1♂ OSUC 618379); 19-VI-1981, N. Tremblay (1♀ MGCL); VI-VII-1981, N. Tremblay (3♂ MGCL); 10-VI-1982, N. Tremblay (1♂ OSUC 618428); no date, N. Tremblay (1♂ OSUC 618405); Dempster Hwy., mi. 45-97, 14-VI-1981, N. Tremblay (1♂ MGCL); Dempster Hwy., mi. 84, 11-VI-1981, N. Tremblay (18♂, 4♀ MGCL); Dempster Hwy., mi. 96, 23-VI-1981, N. Tremblay (2♂ MGCL); Dempster Hwy., mi. 97, 14-VI-1981, N. Tremblay (1♂ MGCL); Dempster Hwy., mi. 97, 18-VI-1981, N. Tremblay (1♀ MGCL); 6-VI-1984, N. Tremblay (1♂ MGCL); Haines Jct., 6-VI-1966 (1♂ MGCL); 9-VI-1966 (4♂ MGCL; incl. SN-15-158); 10-VI-1966 (1♂ MGCL); 12-VI-1966 (3♂ MGCL; incl. SN-15-161); 13-VI-1966 (1♀ MGCL); 16-VI-1966 (1♂, 1♀ MGCL); 17-VI-1966 (1♀ MGCL); 21-VI-1966 (2♂ MGCL); 22-VI-1966 (1♂ MGCL); 24-VI-1966 (1♂, 1♀ MGCL); 25-VI-1966 (4♂, 1♀ MGCL; incl. 3♂ SN-15-160, SN-15-159, SN-15-146); 28-VI-1966 (1♂ MGCL); 29-VI-1966 (9♂, 4♀ MGCL; incl. 1♀ SN-15-148); 1-VII-1966 (1♂, 1♀ SN-15-169 MGCL); 12-VI-1967 (2♂, 1♀ MGCL); 14-VI-1967 (1♂ MGCL); 18-VI-1967, obtained from J. A. Ebner (1♂, CDF); 19-VI-1967, J. A. Ebner (1♂ MGCL); 21-VI-1967, J. A. Ebner (1♂ MGCL); 23-VI-1967, J. A. Ebner (1♂ MGCL); 24-VI-1967, J. A. Ebner (1♂ MGCL); 27-VI-1967, obtained from J. A. Ebner (2♀ CDF); 9-VI-1968 (1♂ MGCL); Haines Rd., mi. 87, 30-VI-1966 (1♀ MGCL); Horse Creek, mi. 12.6 Dawson-Mayo Loop, 24-VI-1964, A. H. Legge (2♂, 1♀ MGCL); 24-VI-1964, D. Eff (5♂, 4♀ MGCL); Hwy. 7, Atlin Rd., 2100', 29-VI-1985, C. D. Ferris (1♂ CDF); Hwy. 11 (Silver Trail), km. 31.5 (SW of Mayo), 27-28-VI-1985, C. D. Ferris (9♂, 3♀ CDF); 4-VI-1987, C. D. Ferris (2♂, CDF); 6-VI-1991, C. D. Ferris (10♂, 3♀ CDF); Jubilee Mtn., 1000-1500m, 5-VII-1977, A. Reif (1♂, 1♀ MGCL); Klondike Hwy., mi. 132, N of Yukon River, 20-VI-1975, D. K. Parshall (1♀ OSUC 618388); Lake Laberge, 30 mi. N Whitehorse, 10-VI-1985, J. & L. Troubridge (4♂ MGCL); 14-VI-1985, T. Kral (4♂ MGCL); 15-VI-1985 (2♂ MGCL); 18-VI-1985, T. Kral (2♂ MGCL); Lake Laberge, Hwy. 2, 46.4 km. N Whitehorse, 11-VI-1981, D. K. Parshall (1♂ OSUC 618439); 1-VII-1981, D. K. Parshall (1♂ OSUC 618442); 1-VII-1982, D. K. Parshall (2♂ OSUC 618390, 618441); 11-VII-1982, D. K. Parshall (1m OSUC 618440); 14-VI-1983, D. K. Parshall (9♂ OSUC 618327, 618408-618415); 15-VI-1983, D. K. Parshall (1♂ OSUC 618322); 23-VI-1983, D. K. Parshall (3♀ OSUC 618378, 618446-618447); 25-VI-1983, D. K. Parshall (3♀ OSUC 618443-618445); 14-VII-1983, D. K. Parshall (3♂, 2♀ OSUC 618455-618459); 6-VI-1984, J. P. Ross (2♀ OSUC 618406-618407); 12-VI-1985 (4♂, 1♀ OSUC 618339, 618448-618451); 13-VI-1985, D. K. Parshall (12♂, 5♀ OSUC 618324, 618331-618338, 618430-618437); 14-VI-1985, D. K. Parshall (3♂ MGCL; 13♂, 14♀ OSUC 618323, 618325, 618340-618354, 618418-618427); 15-VI-1985, D. K. Parshall (5♂, 5♀ OSUC 618321, 618326, 618328, 618355-618359, 618453-618454); 16-VI-1985, D. K. Parshall (4♀ OSUC 618360-618363); 18-VI-1985, D. K. Parshall (6♀ OSUC 618364-618368, 618452); 19-VI-1985, D. K. Parshall (1♂, 4♀ 618369-618373); 20-VI-1985, D. K. Parshall

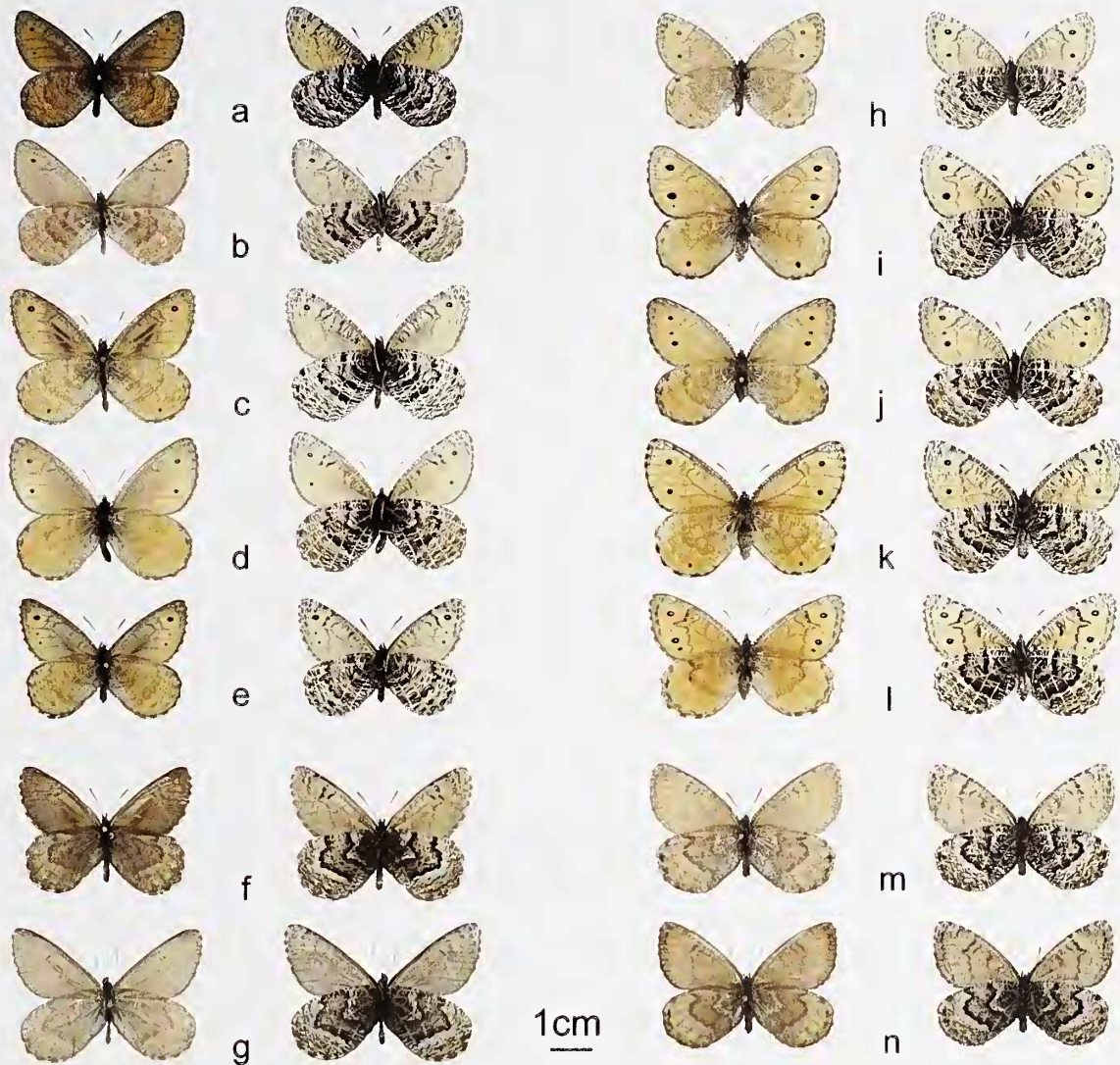


Figure 2. Males (a-e) and females (f-j) of *Oeneis chryxus* from Yukon Territory, Canada, and males (k-l) and females (m-n) of *O. bore* from Alaska (f-g) and Yukon Territory (m-n), in MGCL. Each specimen is figured in dorsal (left) and ventral (right) views. *Oeneis chryxus* from Yukon Territory: a, nr. Snafu Lake on Atlin Rd., 2600', 7 June 1991, J. & F. Preston; b, Dempster Hwy., mi. 97, 14 June 1981, N. Tremblay; c, Dempster Hwy., mi. 10, 10 June 1981, N. Tremblay; d,i,k,l, Campbell Hwy., km. 533, 12 June 1979, J. & F. Preston; e,j, 0.8 mi. N of Lewes Lake Rd. on Hwy. 2, 6 June 1991, J. & F. Preston; h, Whitehorse, 11 June 1966. *Oeneis bore* from: f, Murphy Dome, 17 June 1972, J. & F. Preston; g, Murphy Dome, 16 June 1999, M. Douglas; m, Dempster Hwy., mi. 97, 17 June 1981, N. Tremblay; n, Dempster Hwy., mi. 96, 24 June 1981, N. Tremblay.

(4♀ 618374-618377); Lake Laberge, Hwy. 2, mi. 29, 3-VI-1985, J. Zeligs (1♂ MGCL); 18-VI-1985, J. Zeligs (1♂ MGCL); Mts. SW of Haines Jct. (5-18 mi.), 3-4000', 22-VI-1967 (1♂ MGCL); N of Stewart Crossing, Hwy. 2, 22-VI-1983, [D. K. Parshall] (3♂, 5♀ OSUC 618330 [*this specimen with *O. tanana* barcode, Fig. 10c-d], 618380-618386); N of Stewart Crossing, Klondike Hwy., mi. 24, 20-VI-1975, D. K. Parshall (2♂ OSUC 618329 [*this specimen with *O. tanana* barcode, Fig. 10a-b], 618389); nr. Snafu Lake on Atlin Rd., 2600', 7-VI-1991, J. & F. Preston (4♂ MGCL); St. Elias Mts., Nickel Ck., 14-VI-1985, B. Grooms (1♂ MGCL); Stewart Crossing, Klondike Loop Rd., 1600', 13-VI-1979, J. & F. Preston (1♂, 2♀ MGCL); Twin Lakes, Hwy. 2, km. 115, 14-VI-1983, D. K. Parshall

(2♀ OSUC 618416-618417); 28-VI-1983, D. K. Parshall (1♂ OSUC 618438); Whitehorse, 10-VII-1919, "paratype" of "yukonensis" (1♀ MGCL); 6-9-VI-1923 (1♂ MGCL); 8-VI-1923 (1♂ MGCL); 9-VI-1923 (2♂ MGCL); 17-VI-1923, J. Kusche (2♂ MGCL); 8-VI-1966 (1♂ MGCL); 9-VI-1966, H. Ebner (1♂ MGCL); 10-VI-1966 (1♂ MGCL); 11-VI-1966 (1♀ MGCL); 13-VI-1966 (1♀ MGCL); 2-VI-1982 (1♀ OSUC 618429); 1-VII-1982, B. Grooms (1♂ MGCL); Whitehorse, 2500', 24-VI-1981, G. Anweiler (1♂ CDF); 8-10-VI-1982, J. P. Ross (3♂, 5♀ CDF); Whitehorse, Baxter coll. (1♂ MGCL); Yukon Hwy. 2 (from Skagway, AK), km. 126, 2550', 6-VI-1991, J. & F. Preston (5♂ MGCL); 0.8 mi. N of Lewes Lake Rd. on Hwy. 2, 2700', 6-VI-1991, J. & F. Preston (6♂, 1♀ MGCL); 1.4 mi. S of Lewes Lake Rd.,

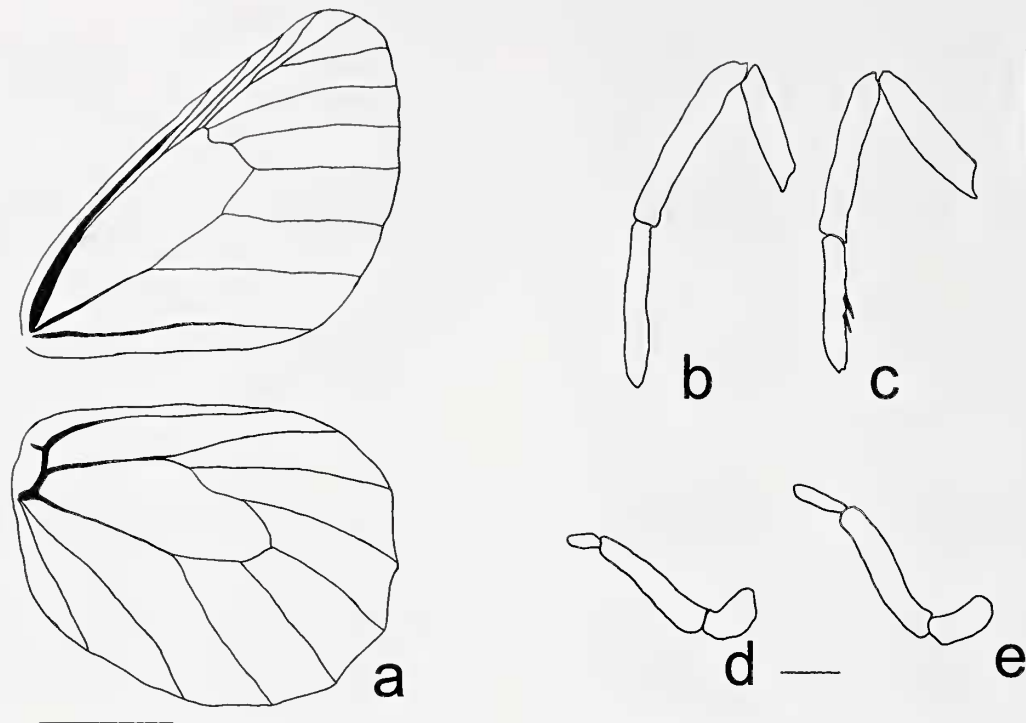


Figure 3. Morphology of *Oeneis tanana* from 5 mi. S of Tok, Alaska: a, male wing venation; b, male foreleg; c, female foreleg; d, male labial palpus; e, female labial palpus. Illustrations by Shinichi Nakahara. Scale bar = 10 mm for a, otherwise 1 mm.

W of Hwy. 2, 2550', 6-VI-1991, J. & F. Preston (1♂, 1♀ MGCL); 20 mi. S Burwash Landing, 1-VII-1948 (1♂ MGCL SN-15-150); "Alaska" [old specimen, most likely from Whitehorse area] (1♂ MGCL). Note: Much of the material from the Haines area, including that attributed to J. Ebner, was likely collected by Dr. A. M. Pearson, who collected for Ebner in the Haines area for several years in the 1960's.

USA: ALASKA: Eagle, 2-VII-1901, S. Hall Young (1♂ MGCL); 27-VI-1903, Reed Heilig, "paratype" of "yukonensis" (1♂ MGCL); Kathul Mtn., N side Yukon River, 6 mi above mouth Kandik R., 29-VI-1975, E. Holsten (3♀ KWP; UAM100379423-UAM100379425); 5-VIII[sic!]-1975, E. Holsten (1♀ KWP; UAM100379422).

Etymology. This butterfly is named for the Tanana River, which flows through southeastern and central Alaska. Tanana is a Koyukon (Athabaskan) word meaning "trail river", though the term is also applied to an Athabaskan indigenous group (Bright 2004).

Diagnosis. Adults of *O. tanana* average larger than those of Yukon *O. chryxus*. The mean forewing length of male *O. tanana* is 26.7 mm (range 24.6 to 29.4 mm, n = 20), vs. 24.8 mm (range 19.6 to 27.4 mm, n = 20) in Yukon *O. chryxus*. Females of *O. tanana* also average larger, with a mean forewing length of 26.9 mm (range 24.9 to 31.3 mm, n = 10), vs. 26.1 mm (range 21.0 to 29.1 mm, n = 10) in Yukon *O. chryxus*. Adults of *O. tanana* can usually be identified by the following traits, compared to Yukon *O. chryxus*: 1) larger size, 2) darker overall upperside coloration, with paler areas dark ochre or reddish, 3) darker ventral forewing coloration, 4) bolder dark ventral hindwing transverse bands, 5) expanded whitish areas on the ventral

hindwing, 6) valvae average more robust. While none of these individual characters are strictly diagnostic, when considered together, essentially all specimens can be reliably identified to taxon. In addition, adults of *O. tanana* are separated from those of Yukon *O. chryxus* by their unique *COI* barcode sequences (but see below), which are identical to those found in adjacent populations of *O. bore*, with the exception of a single base-pair substitution at site 300: G→A (site number corresponds to the sequence given above).

Distribution. All localities where *O. tanana* is confirmed to occur are within the Tanana River Basin, in southeastern and central Alaska, including the lower north slope of the Alaska Range (Fig. 7). Available records suggest that *O. tanana* is widely distributed in appropriate habitats throughout the Tanana River drainage, at least from the Northway area (Northway Airport and Alaska Hwy. mi. 1270), northwest to Nenana, a roughly 400 km. (250 mi.) range centered along the Tanana River. Altitudinal records range from 107 m (351') at Nenana to 635 m (2083') along the Richardson Highway (mi. 229) and Delta River, which drains into the Tanana River to the north. A very small part of the Tanana River Basin extends into Yukon Territory (Moran 2007), but it is unknown if *O. tanana* occurs there. Likewise, it remains unknown how far down the Tanana River Basin *O. tanana* may occur, or if it occurs along the Yukon River Basin downstream or upstream of its junction with the Tanana River at Tanana. Most of this region has not been surveyed for butterflies. All specimens we have examined of *O. tanana* were collected in odd-numbered years, with the exception of a single female from Alaska Highway mile 1371, labeled from 1970. No collector's name is provided on the

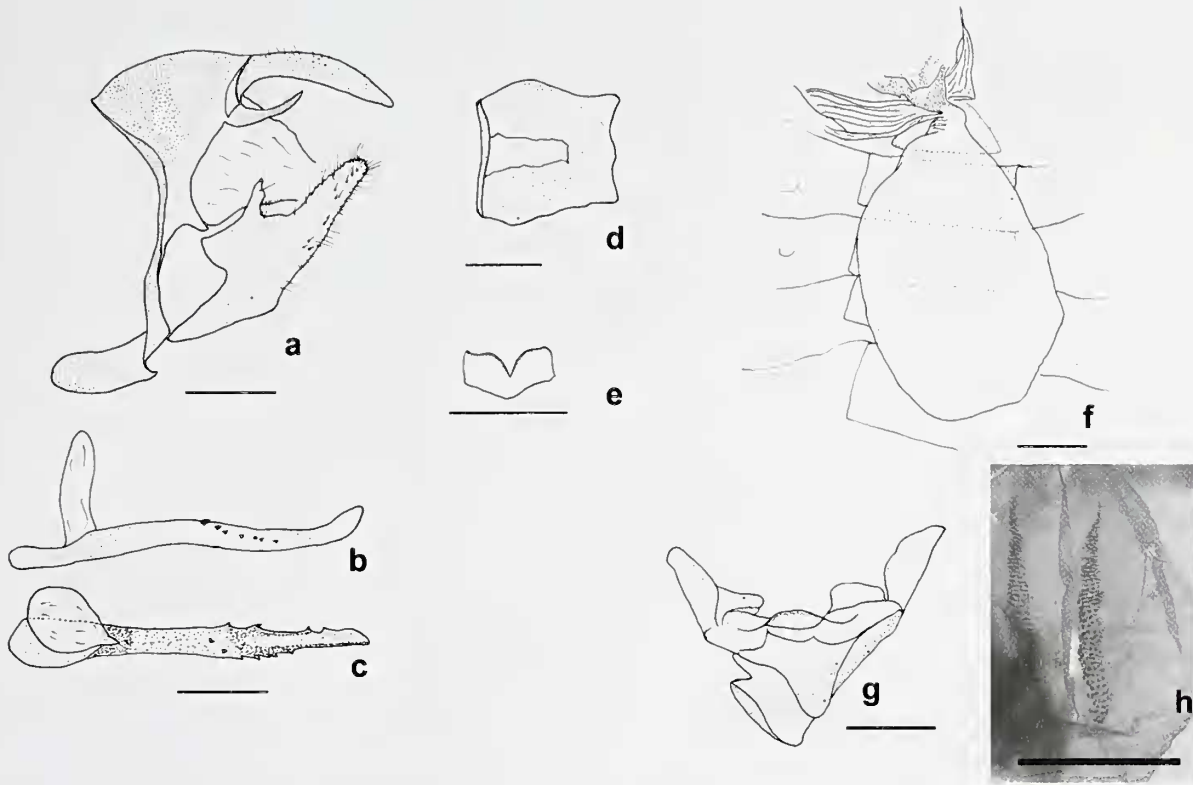


Figure 4. Male and female genitalia of *Oeneis tanana* from 5 mi. S of Tok, Alaska: a, male genitalia (SN-15-156) in left lateral view; b, aedeagus in left lateral view; c, aedeagus in dorsal view; d, eighth tergite in dorsal view; e, juxta in dorsal view; f, female genitalia (SN-15-151) in dorsal view; g, lamella antevaginalis in front view; h, signa. Illustrations by Shinichi Nakahara. Scale bar = 1 mm.

label, and the possibility of a labeling error cannot be ruled out. The earliest specimen of *O. tanana* we have seen is from 18 May (1997, 21 mi. SW Fairbanks), and the latest is from 6 July (1995, 5 mi. S of Tok), with most records from the second and third weeks of June.

Habitat. Adults of *O. tanana* fly in open, dry, grassy areas and clearings in boreal forest. In disturbed areas, they tend to frequent abandoned roads and trails, undeveloped dirt/gravel roads (Fig. 8), and power line cuts. They are fairly sedentary and in response to a disturbance fly short distances, usually in straight lines, to settle again. The butterflies generally sit on the ground or perch on rocks, or on low vegetation, with wings folded over the back unless basking. While colonies are isolated, numerous individuals are frequently present at occupied sites. Aside from grasses, sedges and various arctic forbs, the principal vegetation at the type locality includes black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), quaking aspen (*Populus tremuloides* Michx.), occasional birch (*Betula* sp.), and willows (*Salix* sp.). *Oeneis tanana* flies in sympatry with *O. jutta* (Hübner, [1806]) at Nenana, Alaska Hwy. mi. 1410, and in the vicinity of Tok (including at the type locality), and it flies with both *O. jutta* and *O. philipi* Troubridge, 1988 at Northway Airport. No information on the early stages or larval foodplants of *O. tanana* is known to date, although grasses and/or sedges presumably serve as the larval foodplants, as reported for other taxa in the *O. chryxus* complex (James & Nunnallee 2011).

DISCUSSION

Like *O. chryxus*, the genitalia of *O. tanana* possess a tooth-like projection of the dorsal margin of the valva, denticles on the valva in a single series, a strongly sclerotized ventral swelling of the lamella antevaginalis, and a left-skewed vertical plate of the lamella antevaginalis. Lukhtanov & Eitschberger (2001) noted the first three of these characters as diagnostic of the *bore* group. Based on the presence of these characters, *Oeneis tanana* is clearly a member of the *bore* group. Despite the phenotypic differences (adult size and wing color and pattern) between *O. tanana* and *O. chryxus*, the genitalia of these two species are very similar. Subtle differences in genitalia of both sexes indicated in Figs. 4-5 apparently reflect individual variation. To date, we have not identified any diagnostic characters in the genitalia that serve to unambiguously separate these two taxa, although the valvae of *O. tanana* average somewhat more robust than those of *O. chryxus* (Fig. 6), and are generally

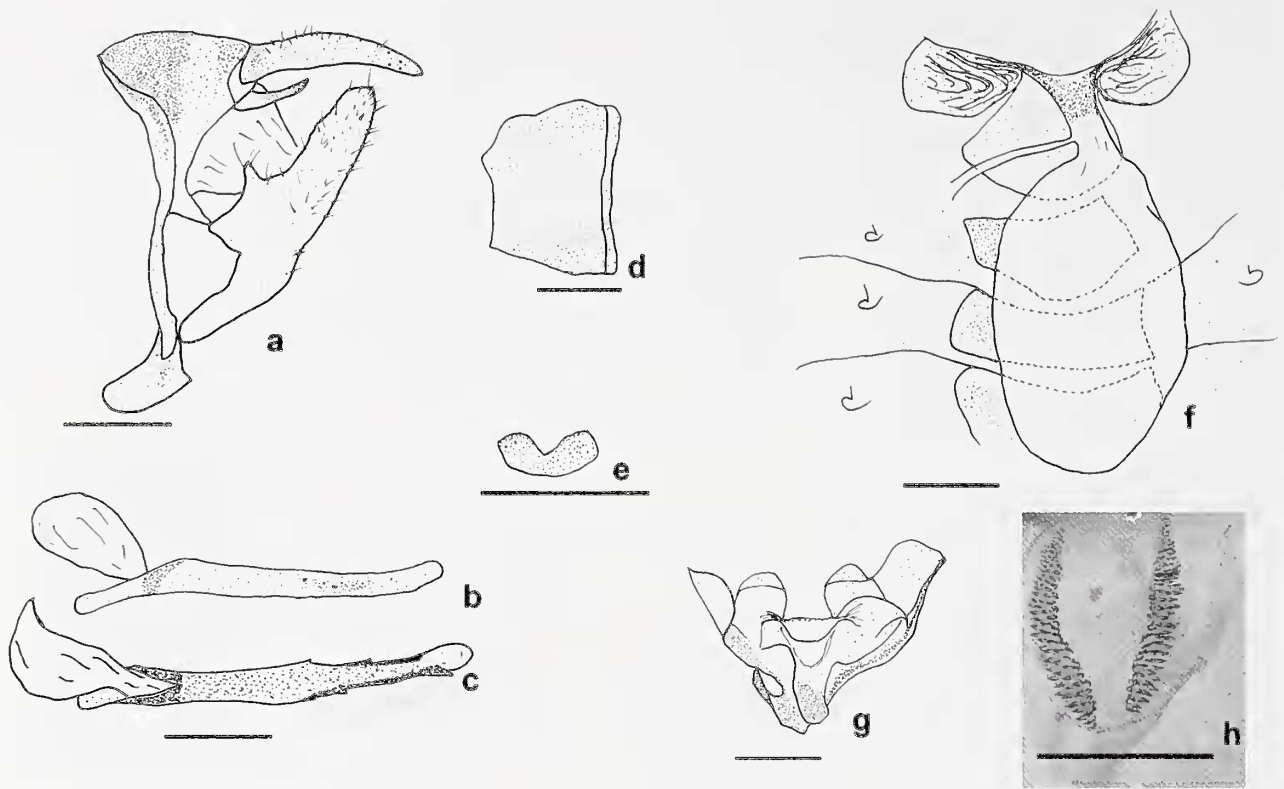


Figure 5. Male and female genitalia of *Oeneis chryxus* from Haines Junction, Yukon Territory, Canada: a, male genitalia (SN-15-158) in left lateral view; b, aedeagus in left lateral view; c, aedeagus in dorsal view; d, eighth tergite in dorsal view; e, juxta in dorsal view; f, female genitalia (SN-15-169) in dorsal view; g, lamella antevaginalis in front view; h, signa. Illustrations by Shinichi Nakahara. Scale bar = 1 mm.

slightly larger than those of *O. bore*. This result is not surprising, considering the lack of consistent genitalic differences reported among other North American members of the *bore* group. On the other hand, female genitalia of *O. tanana* and *O. chryxus* differ from those of *O. bore* by the position of the vertical projection of the lamella antevaginalis, which is skewed to the left in *O. tanana* and *O. chryxus*. Thus, genitalic characters suggest that *O. tanana* is morphologically closer to *O. chryxus* than *O. bore*, although the molecular data discussed below indicate the opposite.

Very little information on *O. tanana* is available in the literature. We are not aware of any previously published images of adult or immature *O. tanana*, other than the very recent images of adults of both sexes (as *O. chryxus caryi*) by Philip & Ferris (2015). Distributional records for *O. chryxus* in Alaska provided by Philip (1996, 1998, 2006) and Magoun & Dean (2000) all refer to *O. tanana*; we have examined specimens from all but one of these sites. The only molecular study that has focused on the *chryxus*

complex is that by Nice & Shapiro (2001), who studied haplotype variation in 440 base pairs of mitochondrial *COII* among various western USA populations. Many samples were analyzed from California (*O. c. ivallda* and *O. c. stanislaus*), with others from Idaho, Nevada, Montana, Utah, Colorado, and New Mexico, as well as two specimens from Tok, Alaska (all considered to be *O. c. chryxus*). The specimens from Tok (now recognized as *O. tanana*) were found to possess a unique haplotype (type 'E') not shared with any other populations in the analysis, but no discussion of this population or haplotype was provided.

***COI* barcode analysis and morphology of the *chryxus* complex**

The dendrogram resulting from our analysis of *COI* barcode sequences (Fig. 9) is complex, yet largely corroborates traditional treatments of the *bore* group based on morphology. *Oeneis alberta*, which was included in initial analyses, was omitted from our

final tree since it appears polyphyletic, invariably sharing *bore* group haplotypes, yet its status as a species-level taxon, closely related to *O. chryxus*, has not been challenged. The close relationship between *O. bore* and *O. chryxus*, as suggested by many authors based on similarities in the male genitalia (e.g., Elwes & Edwards 1893; Gross 1970; Gorbunov 2001; Lukhtanov & Eitschberger 2001), is corroborated by our analysis, in that the taxa don't appear reciprocally monophyletic. These irregularities in barcodes are likely a reflection of evolutionary closeness of taxa within the *bore* group and are possibly the result of mitochondrial introgression. This scenario would presumably explain the placement of *O. nevadensis* barcodes as derived within the *chryxus* complex, while *O. macounii* sequences are basal to all of these. All indications from morphology suggest that *O. nevadensis* and *O. macounii* are sister taxa, and their close relationship has not been questioned. Despite being obscured by apparent introgression, groupings on the dendrogram do appear to be highly informative, and may be indicative of cryptic diversity within the *chryxus* complex.

Oeneis chryxus is distributed among five barcode clusters, which closely correspond with morphological and biogeographical attributes. The first group includes the Rocky Mountain *O. chryxus* populations, comprising *O. c. chryxus*, with samples included from Colorado, Montana, Alberta, British Columbia, and Yukon Territory (see discussion below regarding Yukon material). These sequences are the least derived of the *chryxus* complex, as also indicated for *COII* by Nice & Shapiro (2001). Across this range, *O. c. chryxus* shows various degrees of localized morphological diversification, but barcodes suggest that all of these populations are very closely related. While not included in this study, the southernmost Rocky Mountain population, *O. c. socorro*, described from Mt. Withington, Socorro County, New Mexico, appears to be closely related to typical *O. c. chryxus* to the north (Holland 2010), based on morphology, habitat, and distribution, although an affiliation with *O. c. altacordillera* (see below) cannot yet be ruled out.

The second barcode group of the *chryxus* complex includes just *O. c. valerata*. This taxon is endemic to alpine habitats in the Olympic Mountains of Washington. While Burdick (1958) cited similar material from Vancouver Island, we know of no valid records from there. The presence of this taxon in its own barcode group suggests it is genetically rather distinct from other groups in the *chryxus* complex, presumably as a result of a long history of isolation on the Olympic Peninsula.

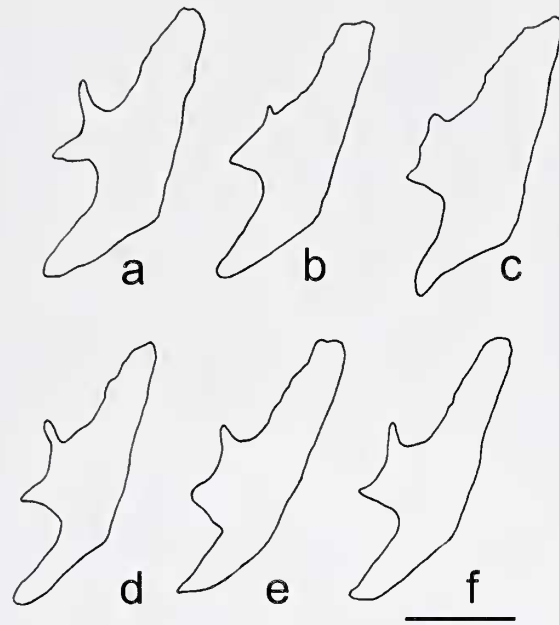


Figure 6. Variation in valvae of *Oeneis tanana* and *O. chryxus*: a-c, *Oeneis tanana* (SN-15-145; SN-15-155; SN-15-157); d-f, *Oeneis chryxus* (SN-15-158; SN-15-159; SN-15-160). Illustrations by Shinichi Nakahara. Scale bar = 1 mm.

The third barcode cluster includes the Sierra Nevada taxa *O. c. ivallda* and *O. c. stanislaus*, together with a single specimen of *O. c. chryxus* from Utah. Many authors have treated the pallid *O. c. ivallda* as a species-level taxon while considering *O. c. stanislaus* to be a subspecies of *O. chryxus*, based on its similar tawny coloration (e.g., dos Passos 1961, 1964; Gross 1970; Murayama 1973; Emmel 1975; Miller & Brown 1981; Pyle 1981; Garth & Tilden 1986; Tilden & Smith 1986). These taxa were studied in detail by Porter & Shapiro (1991) and Nice & Shapiro (2001), who found that they are very closely related, clearly conspecific as treated by Hovanitz (1937, 1940), and likely resulted from Pleistocene colonization of the Sierra Nevada via dispersal from the Rocky Mountains across the Great Basin. Our results corroborate these conclusions, as *O. c. ivallda* and *O. c. stanislaus* are not separable based on barcode sequences. In addition, the inclusion of a single Utah specimen in this group is consistent with the notion that Sierra Nevada populations originated through cross-Great Basin dispersal, and some haplotypes are apparently still shared (Nice & Shapiro 2001).

The fourth barcode cluster includes the boreal North American taxa *O. c. calais* and *O. c. strigulosa*, with samples included from Michigan, Ontario and

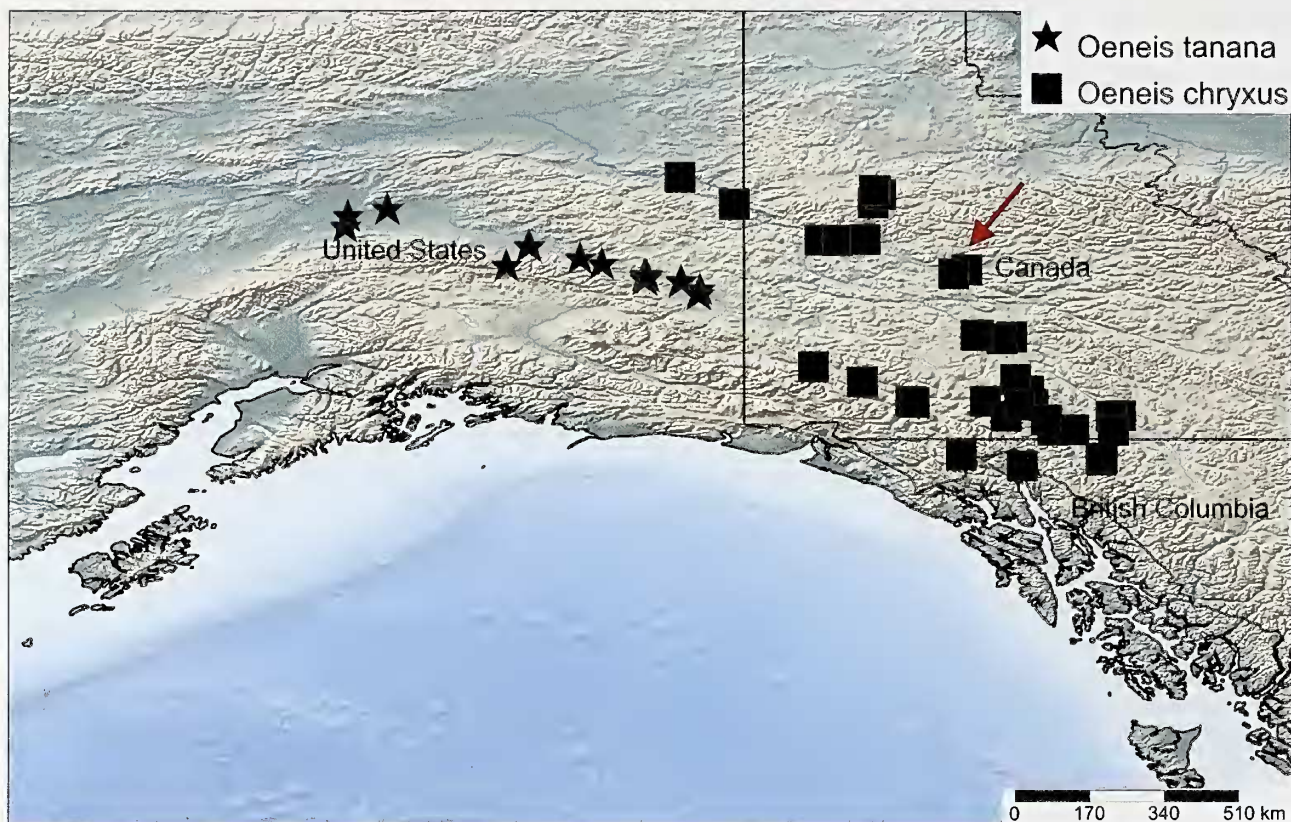


Figure 7. Distribution of *Oeneis tanana* (stars) and *O. chryxus* (squares) in Alaska and northwestern Canada. Red arrow indicates the Stewart Crossing area, Yukon Territory, where a few individuals with *O. tanana*-type *COI* sequences have been found (see discussion in text).

Manitoba. These two taxa are very closely related; it is often not possible to separate them in collections other than by locality, and barcodes failed to clearly distinguish them. This group occupies the central and northeastern North American boreal forests, from Quebec and Ontario, westward into Northwest Territories and northern Alberta, and it appears to be allopatric with respect to the distribution of *O. c. chryxus* in Alberta and British Columbia (Bird et al. 1995; Guppy & Shepard 2001), although access to most regions of potential sympatry or parapatry is extremely limited. As discussed below, the holotype specimen of *O. c. caryi* is fairly typical of specimens found in the western populations of this group. *Oeneis. c. calais* (including *O. c. strigulosa* and/or *O. c. caryi*) has been considered a species-level taxon by various authors (Scudder 1865; Cary 1906; Scott 2006; Kondla 2010).

The fifth cluster of the *chryxus* complex is the recently described *O. c. altacordillera*. This taxon inhabits high-elevations in the southern Rocky Mountains, generally above 3048 m (10,000') elevation, and is frequently found at or just above treeline. While its overall

distribution remains to be determined, it appears to be endemic to Colorado and perhaps northern New Mexico (Warren 2011), yet adults from some populations in Colorado are not easily assignable to either taxon based on wing morphology (Scott 2006; pers. obs. ADW 2015). Given the marked difference in barcode haplotypes between typical *O. c. altacordillera* and *O. c. chryxus* from lower elevations in Colorado and elsewhere in the Rocky Mountains (also see Nice & Shapiro 2001), an extensive barcode survey will likely resolve questions about the overall distribution of *O. c. altacordillera*, as well as the identity of the lectotype of *O. c. chryxus* (Shepard 1984; Scott 2010). While Scott (2006) described *O. c. altacordillera* as a subspecies of *O. c. calais* (which was treated as a species-level taxon), an arrangement followed but questioned by Kondla (2010), our results suggest the two taxa are not very closely related, and that *O. c. altacordillera* may best be considered a species-level taxon.

Oeneis tanana is positioned in our dendrogram (Fig. 9) as the most derived grouping within a clade of Arctic American *O. bore.* All five barcode sequences

obtained from Alaskan *O. tanana*, from three sites in the Tanana River Valley, were identical, and differ from those of nearby populations of *O. bore* by a single base-pair at site 300: G->A. This is a non-synonymous substitution, which translates to a S->N substitution in protein. The significance of this is not yet known.

Upon searching the BOLD database (Ratnasingham & Hebert 2007), we found a single sequence (HBNK245-07) of *Oeneis* from Yukon Territory that is a perfect match to those of *O. tanana*, from along the Stewart River (and Silver Trail) near Mayo. We therefore obtained barcodes from five additional specimens taken nearby, from the vicinity of Stewart Crossing, approximately 40 km. (24 mi.) southwest of Mayo, also along the Stewart River. Two of these specimens, from “N of Stewart Crossing” (Fig. 10, from OSUC) also possess barcodes typical of *O. tanana*, while three others, from “Stewart Crossing” (MGCL) have barcodes like those of other *O. chryxus* in Yukon Territory. The two specimens (Fig. 10) with barcodes typical of *O. tanana* are fairly dark above, compared to other *O. chryxus* from the province (Fig. 2), and have a ventral hindwing banding pattern reminiscent of Alaskan *O. tanana*, yet they are smaller and somewhat tawnier above than most Alaskan *O. tanana*. The three specimens with barcodes of *O. chryxus* are tawnier above and have a less contrasting ventral hindwing pattern; they appear typical of other *O. chryxus* specimens from the region. A much larger sampling of barcodes from populations in the area will be needed to determine if variation in phenotypes correspond to differences in barcode haplotypes.

The significance of the presence of barcode haplotypes typical of *O. tanana* among specimens from along the Stewart River in Yukon Territory remains unknown. It could indicate that *O. tanana* occurs disjunctly in Yukon Territory, perhaps as a somewhat smaller and tawnier form, at least along the Stewart River, in exact or near sympatry with *O. chryxus*. It could also indicate that haplotypes of *O. tanana* have introgressed into some Yukon populations of *O. chryxus*, but that only one phenotypically variable species actually occurs in the Stewart River area. Extensive study of populations along the Stewart River and nearby regions of central Yukon Territory will be needed to resolve this issue.

Taxonomic status and distribution of Yukon-Alaska *Oeneis chryxus*

Oeneis chryxus is widely distributed in Yukon Territory, with records from even and odd-numbered years, where it inhabits dry, open barrens and subarctic steppe (Ferris et al. 1983; Lafontaine & Wood 1997).



Figure 8. Habitat of *Oeneis tanana*, 8 miles south of Tok, Alaska, 25 June 2007. Photo by David Shaw.

Various authors have considered Yukon populations of *O. chryxus* to represent *O. c. caryi* (Layberry et al. 1998; Guppy & Shepard 2001), although Burdick (1958) noted that this is incorrect. The type specimen of *O. c. caryi*, as figured by Burdick (1958) and Warren et al. (2015), is markedly different than any material we have examined from Yukon Territory, and, other than the enlarged forewing ocelli, appears to fall within the normal range of variation seen in the western populations of *O. c. calais*. Further studies are needed to confirm the taxonomic status of *O. c. caryi*, although we believe *O. c. caryi* should probably be considered synonymous with *O. c. calais*; alternatively, if *O. c. calais* is considered to be a species-level taxon, *O. c. caryi* might be considered its western subspecies, as implied by McDunnough (1934) and treated by Kondla (2010).

Thus, the name *O. c. caryi* does not apply to populations of *O. chryxus* in northern British Columbia, Yukon Territory, or those barely entering eastern Alaska (see below). While the erection of a new subspecies name might be justifiable for these populations, we feel they are close enough to nominotypical *O. chryxus* in phenotype to tentatively associate them with that taxon. The similarity of *COI* sequences between Yukon and Rocky Mountain material to the south (British Columbia, Alberta, Montana, Colorado) also supports this arrangement, given that barcodes from Yukon specimens are extremely similar or identical to those from further south in the Rocky Mountains.

Oeneis chryxus was first reported from Alaska by Holland (1900), based on a single female taken at

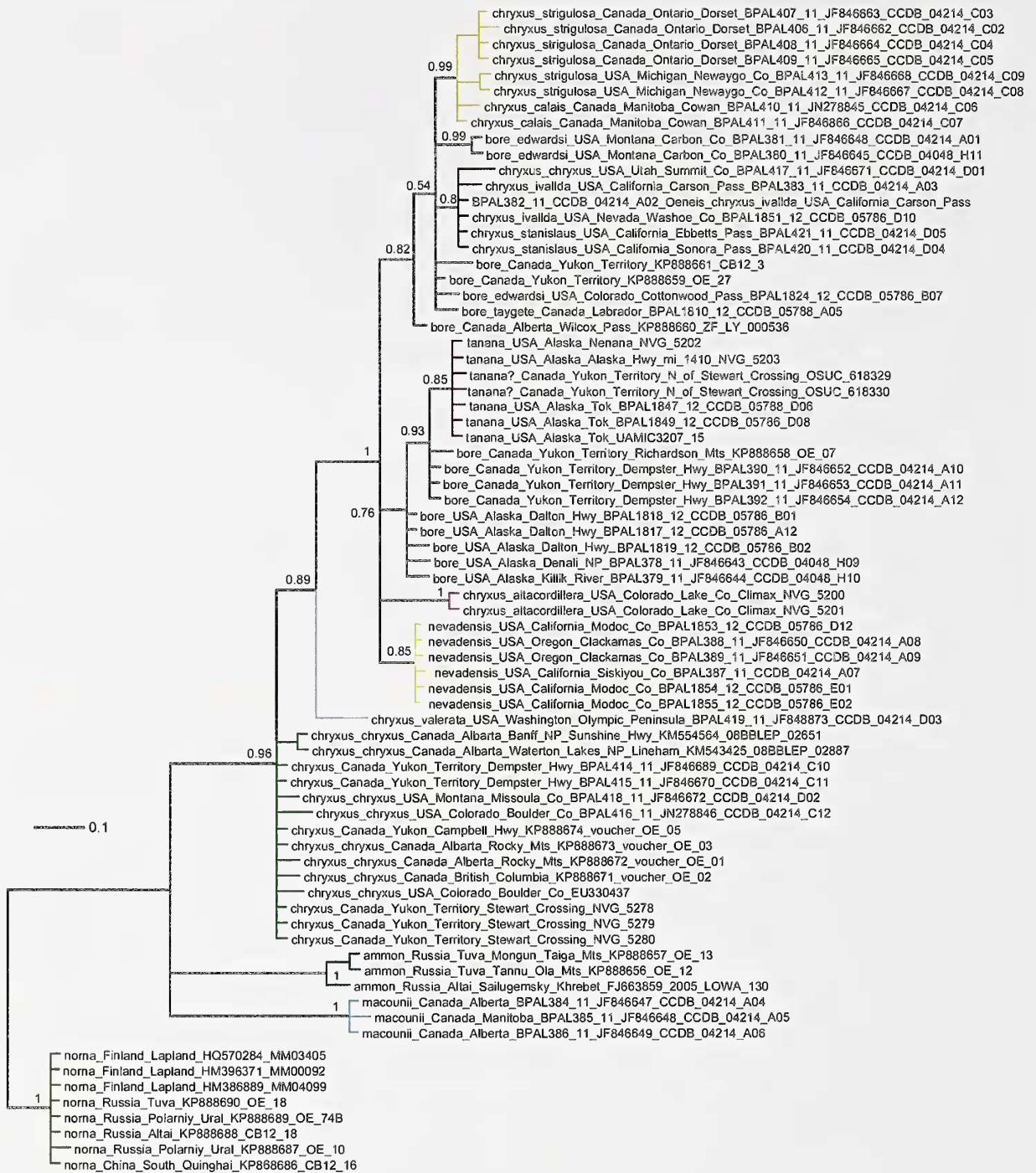


Figure 9. Dendrogram generated from Bayesian analysis of *COI* barcode sequences from taxa in the bore group of *Oeneis*, with *C. norma* as the outgroup. See text for details of the analysis. Colored groupings identify taxa and populations discussed in the text.

Eagle City, on 10 July 1899, by Reverend S. Hall Young. We have examined two male specimens from Eagle, one collected by Young in 1901, and another collected by Reed Heilig in 1903, both of which are typical of *O. chryxus* found to the east in Yukon Territory. One of the specimens bears a blue “paratype” label reading “klondikensis FC”, affixed by Frank Chermock. This name was never formally proposed, but was apparently intended to represent *O. c. “caryi”* of recent authors (e.g., Layberry et al. 1998; Guppy & Shepard 2001). The “holotype” and “allotype” of “klondikensis”, which we also examined, are from Dawson, Yukon Territory, and a second “paratype” we examined is from Whitehorse. More recently, Guppy & Shepard (2001) indicated the presence of *O. chryxus* in the Alaska Panhandle, in the vicinity of Skagway. While we have not examined specimens from this area, this material is likely to be morphologically like adjacent *O. chryxus* populations in southern Yukon Territory and far northwestern British Columbia.

Thus, with the delimitation of *O. tanana*, it appears that *O. chryxus* just barely penetrates into Alaska from Yukon Territory, along the Yukon River corridor, where it is known from two sites just 9.5 km. (5.9 mi.- at Eagle) and 60 km. (37 mi.- at Kathul Mtn.) west of the Canadian border (Fig. 7). Despite considerable collecting efforts by various researchers along the Taylor and Steese highways, which traverse the Yukon-Tanana uplands separating the Yukon and Tanana rivers, *O. chryxus* remains unreported from the region (the record from the central Yukon-Tanana highlands indicated by Philip and Ferris (2015) represents a misplaced Kathul Mountain record). Likewise, *O. chryxus* appears to barely extend into the Alaska Panhandle near Skagway, presumably from widespread populations just to the north in northwestern British Columbia.

Oeneis tanana appears to be allopatric with respect to *O. chryxus* in Alaska, and it might be endemic to Alaska (but see above). Available records suggest that Alaskan *O. tanana* populations are separated from the nearest known population of *O. chryxus* in Alaska (at Eagle) by about 185 air km. (115 mi.), and are separated from the nearest known population of *O. chryxus* in Yukon Territory (at Nickel Creek) by about 210 air km. (130 mi.).

Hypothesized evolutionary history of *Oeneis tanana*

The confirmed distribution of *Oeneis tanana* lies within the Tanana River Basin in Alaska, most or all of which was apparently never glaciated during the last glacial maximum in the late Pleistocene, roughly 28,000 to 14,000 years ago (Dyke 1999;

Goetcheus & Birks 2001; Harrington 2005). During this time, the Tanana River Basin, together with the larger and contiguous Yukon River Basin (including lower elevations along the Yukon River drainage in northern and central Yukon Territory) formed the southeastern limits of eastern Beringia (*sensu* Elias & Brigham-Grette 2007), a region widely recognized as a refugium for many plants and animals during the glacial cycles of the Pleistocene (e.g., Guthrie 2001; Pruett & Winker 2005; Geml et al. 2006; Zazula et al. 2006; Elias & Brigham-Grette 2007; Fritz et al. 2012; DeChaine et al. 2013; Edwards et al. 2014). The Tanana and Yukon River basins were identified as distinct sub-refugia during the Pleistocene for two fish taxa (Stamford & Taylor 2004; Campbell et al. 2015), and four species of trees (Roberts & Hamann 2015), and we believe the region likely served as a refugium for *O. tanana* as well.

We hypothesize that during the last glacial maximum, *O. tanana* persisted in the Yukon-Tanana basins, while *O. chryxus* was isolated in a southern Rocky Mountain refugium, similar to what has been documented for *Rhodiola integrifolia* Raf. (Crassulaceae) (DeChaine et al. 2013). Under this scenario, *O. chryxus* dispersed northward along the Rocky Mountain cordillera as the ice sheets retreated, while *O. tanana* remained within the Yukon-Tanana basins. This scenario is supported by the close similarity of *COI* barcode haplotypes among cordilleran *O. chryxus* from Colorado to Yukon Territory (also see Nice & Shapiro 2001), and uniqueness of *O. tanana* haplotypes, although the possibility of isolated refugia for *O. chryxus* in the northern Rocky Mountains cannot be ruled out (Marr et al. 2008; Savidge 2012). We hope that this hypothesis will be investigated in the future in a detailed phylogeographic study.

Given the similarity of *COI* haplotypes between *O. tanana* and Arctic American populations of *O. bore*, introgression between the two taxa has likely occurred, perhaps during the Pleistocene. Although adults of *O. tanana* average consistently larger than those of nearby *O. bore*, the ventral hindwing pattern of *O. tanana* is often inseparable from that of *O. bore*, due to the bold transverse bands and broad whitish areas bordering them. The dark dorsal coloration of *O. tanana* is also suggestive of *O. bore*. While overall, the morphology of *O. tanana* is seemingly closer to that of *O. chryxus* than to *O. bore*, these traits, as well as the *COI* haplotypes, suggest some degree of influence from *O. bore*. While much additional study is required, we feel it is possible that *O. tanana* could have evolved through hybridization between *O. bore* and *O. chryxus*; this highly speculative hypothesis

should be tested through molecular studies. While such a mode of speciation is widely accepted in plants (e.g., Soltis 2013), it has only recently been seriously investigated in animals, including butterflies (Gompert et al. 2006; Mavárez et al. 2006; Mallet 2007; Kunte et al. 2011; Abbott et al. 2013; Dupuis & Sperling 2015; Lukhtanov et al. 2015).

Taxonomic rank for *Oeneis tanana*: species or subspecies?

The last two new “species” of *Oeneis* described from North America (Troubridge et al. 1982; Troubridge & Parshall 1988) have proven to be very closely related to or conspecific with described taxa in the northeastern Palearctic region. *Oeneis excubitor* Troubridge, Philip, Scott & J. Shepard, 1982 has been treated as a subspecies of *O. alpina* Kurentsov, 1970 by most subsequent authors (Scott 1986; Lafontaine & Wood 1997; Layberry et al. 1998; Warren et al. 2015). *Oeneis philipi* has apparently close relatives in the northeastern Palearctic, sometimes called *O. rosovi* Kurentsov, 1970, a name that has been applied as a senior synonym of *O. philipi* (Lafontaine & Wood 1997; Lafontaine & Troubridge 1998; Layberry et al. 1998). However, as noted by Lukhtanov (1989), the two syntypes of *O. rosovi* appear to represent two different species, so until a lectotype is designated, the application of this name to any populations remains problematical (Pelham 2008). *Oeneis tanana*, in contrast, does not appear to have any close relatives in the Palearctic; its overall morphology and *COI* haplotypes clearly place it within the bore group, apparently most closely related to the entirely Nearctic *chryxus* complex.

When we initiated this project, we held no preconceived notions about the taxonomic rank of *O. tanana*. All we knew, based on overall morphology of large series of adults, is that they were different from *O. chryxus* in Yukon Territory. As our investigation progressed, and molecular and biogeographic information was analyzed from other members of the *chryxus* complex, we eventually determined that, based on currently available information, *O. tanana* is best considered a species-level taxon. The apparent lack of discrete genitalic characters to separate *O. tanana* from other members of the *chryxus* complex is not surprising in the genus *Oeneis*, since closely related species frequently cannot be reliably distinguished via genitalic morphology (e.g., Troubridge & Parshall 1988). While *O. tanana* is apparently allopatric with respect to *O. chryxus* in Alaska, its barcode haplotype is quite distinct from those found in cordilleran *O. chryxus*, and almost all adults examined from Alaska are easily separated from Yukon-Alaska *O. chryxus*

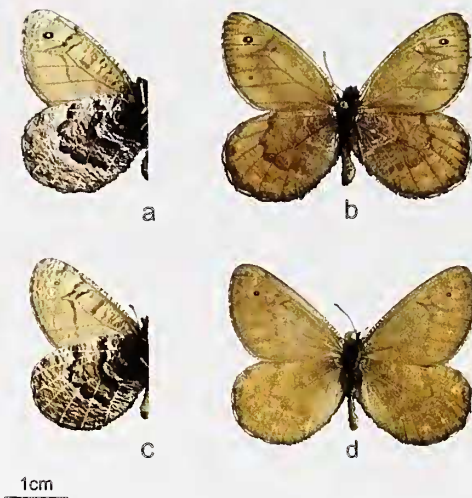


Figure 10. Male *Oeneis* from north of Stewart Crossing, Yukon Territory, Canada, possessing *COI* barcode sequences typical of Alaskan *O. tanana*: a-b, 20 June 1975, D. K. Parshall, OSUC 618329; c-d, 22 June 1983, D. K. Parshall, OSUC 618330. Photos courtesy of Luciana Musetti.

based on their wing morphology. Only the very smallest and tawniest Alaskan individuals of *O. tanana* (e.g., Fig. 1e,k) can potentially be mistaken for Yukon-Alaska *O. chryxus*. Yet in these situations, *O. tanana* tends to have bolder ventral hindwing markings than what is normally seen in Yukon-Alaska *O. chryxus*.

However, many questions remain about the overall distribution of *O. tanana* with respect to *O. chryxus*. The apparent gap of 210 km. in distributions of the two taxa along the Alaska Highway centered on the Yukon – Alaska border should be carefully studied for the possible occurrence of either species or intermediate forms. Likewise, additional surveys along the lower Tanana River, and along the Yukon River downstream of the Kathul Mountain area in Alaska should be conducted to detect the possible occurrence of members of the complex. In addition, populations along the Yukon River and its tributaries in Yukon Territory should be carefully studied and barcoded to determine the significance of *O. tanana* barcodes in the region. Thus, future studies could reinforce our hypothesis that *O. tanana* represents a species-level taxon, or they could indicate that subspecies-level status for *O. tanana* may be more appropriate.

While much additional study of the *O. chryxus* complex, employing multiple genetic markers and additional surveys in remote regions, will be required to fully understand relationships within the group, our

results suggest that *O. chryxus* of most contemporary authors may comprise five species-level taxa: *O. chryxus* (including *O. c. ivallda*, *O. c. stanislaus*, *O. c. chryxus*, and presumably *O. c. socorro*), *O. calais* (including *O. c. strigulosa* and *O. c. caryi*), *O. valerata*, *O. altacordillera* and *O. tanana*, with *O. tanana* apparently being the most distinctive of them all, morphologically. It is also possible, based on available data, to argue that the Sierra Nevada taxa (*O. c. ivallda* and *O. c. stanislaus*) represent a sixth species-level taxon, closely related to *O. chryxus*.

On the other hand, the main groupings in the *chryxus* complex can be interpreted as subspecies-level taxa, depending on one's species concept; indeed, none of them appear to be sympatric in distribution, with the possible exceptions of *O. c. chryxus* and *O. c. altacordillera* in Colorado, *O. c. chryxus* and *O. c. calais* in Alberta, and *O. chryxus* and *O. tanana* in Yukon Territory. Under this scenario, *O. chryxus* would be considered a diverse array of mainly allopatric populations, each of which possessing unique genetic attributes and sometimes highly divergent wing morphologies, distributed across a broad range of habitat types and biogeographical regions in North America. However, as noted above, recent authors have treated *O. c. calais* (including *O. c. strigulosa* and *O. c. caryi*) as a species-level taxon, which our results suggest is a reasonable interpretation. Based on our current knowledge, if *O. c. calais* is considered a species-level taxon, distinct from *O. chryxus*, the other main groupings within the *chryxus* complex should also be treated at the species-level, at least including *O. c. valerata*, *O. c. altacordillera* and *O. tanana*, which appear to be the most divergent members of the complex.

Regardless of its taxonomic status as a species or subspecies, *O. tanana* represents a unique entity within the genus *Oeneis* which deserves much additional study. A better understanding of its evolutionary history may be helpful in understanding mechanisms of diversification within the genus, both in the Nearctic and Palaearctic regions, and may further elucidate the geological history of eastern Beringia. Placing a name on this entity, as we have done herein, is the first step in this process.

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